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The curse of physiology—challenges and opportunities in the interpretation of geochemical data from mollusk shells

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Abstract Physiology corrupts geochemical records of mollusk shells in many ways, e.g., by actively controlling the incorporation of trace elements in the skeleton. However, the effects of variable biomineralization rates and growth cessation have largely remained unconsidered. Mediated by endogenous timekeeping mechanisms, mollusks stop growing skeletal material on a regular basis ranging from ultradian to annual timescales. During growth cessation, the shells do not record environmental conditions. Shell growth also stops when environmental conditions are beyond the physiological tolerance of the organism, e.g., above and below genetically determined, species-specific thermal extremes where shell growth slows and eventually ceases. Such growth disruptions can occur at non-periodic time intervals. Due to growth retardations and halts, proxy records of mollusk shells are thus incomplete, and reconstructed environmental amplitudes prone to truncation. Furthermore, environmental records are biased toward the physiological optimum of the animal. Favorable environmental conditions increase shell growth, whereas adverse environmental conditions result in reduced shell production and lowered overall metabolism. Not least, the duration of the growing season and overall growth rate decrease as the mollusk grows older. Mathematical modeling approaches can significantly improve proxy records obtained from mollusk shells. For example, if the duration of growth cessation is known, it may be possible to model the missing environmental record. It is also fairly easy to account for age-related growth trends, or variable time-averaging in different portions of the shell. However, a major premise for a reliable interpretation of proxy records from a mollusk shell or other organisms secreting biogenic hard parts is a proper understanding of the physiology, and of course, a high-resolution record of the many different environmental factors that may influence physiology and shell growth. The present paper reviews examples from the literature, and unpublished data on how physiology influences geochemical proxy records from mollusk shells, and presents methods how to eliminate such adverse effects.

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Introduction

Shells of mollusks provide high-resolution and temporally aligned records of past climate change (Williams et al. 1982; Jones et al. 1989; Weidman et al. 1994; Wanamaker et al. 2008), as well as seasonality and weather (Surge et al. 2003; Ivany et al. 2004; Kaandorp et al. 2005). Environmental fluctuations are manifested in the shell carbonate in the form of variable growth rates and chemical properties. For example, elevated ambient temperature can result in increased shell production (Jones 1980; Kennish and Olsson 1975; Jones et al. 1989), more negative oxygen isotope values (Epstein and Lowenstam 1953; Mook and Vogel 1968; Krantz et al. 1987; Wefer and Berger 1991), and co-varying strontium and magnesium contents in the shells (Dodd 1965; Stecher et al. 1996).

Aside from the environment, physiology is the other factor that exerts a major control over the mode of how environmental changes are recorded in the shell. One facet of physiology is the so-called vital effect (Urey et al. 1951). This term refers to metabolic processes that modify the chemical composition of the carbonate-secreting fluid, and